Technical Bulletin No. 925 • *November 1946*

UNITED STATES
DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

Growth and Rubber Accumulation in Guayule as Conditioned by Soil Salinity and Irrigation Regime[1]

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CONTENTS

THE ACREAGE of guayule in the Southwestern States was increased extensively during 1942 through the efforts of the Emergency Rubber Project. Many areas in the irrigable valleys of this region contain soil that is either saline or subject to salinization. It was almost inevitable, therefore, that some of the guayule plantings should have been made on slightly to moderately saline soils. Investigators of the Emergency Rubber Project working with guayule early recognized that the growth response of the plant was modified by soil salinity and that the plants were even killed in certain spots where the salt concentration of the soil was moderately high. These investigators also recognized the desirability of a quantitative study of the salt tolerance of the plant, since such information was not available in the literature. In order to supplement their field observations, they called the attention of the salinity laboratory to the need of such studies. Consequently, the investigation comprising this report was undertaken.

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[1] Submitted for publication May 1946. This work was performed under an allotment from the Special Research Fund authorized by Title I of the Bankhead-Jones Act of June 29, 1935, and in cooperation with the ...ltural experiment stations of Arizona, California, Colorado, Idaho, ... Nevada, New Mexico, Oregon, Utah, Washington, Wyoming, ... of Hawaii.

Since sodium chloride ($NaCl$) and sodium sulfate (Na_2SO_4) are the most common salts that occur in saline soils, it follows that these two salts should be included in studies of salt tolerance of plants. It also seemed desirable that laboratory studies on salt tolerance of guayule should be made with a saline soil on which this crop was being grown. Since the effect of salt content of a soil upon plant response is conditioned by the status of the soil moisture, it was considered expedient to incorporate variations in the soil-moisture regime into this experiment.

EXPERIMENTAL PROCEDURE

The sample of Panoche loam used in this study was supplied by the United States Forest Service and was obtained 13½ miles east of Coalinga in Fresno County, Calif., from a tract planted to guayule. At this location the top 18-inch horizon was found to be a light brownish-gray, friable, and slightly calcareous loam that was very porous and low in organic matter. The 4 tons of soil that made up the sample were taken from the upper 10-inch horizon. Laboratory examination indicated that this soil contained 0.85 percent $CaCO_3$. The exchange capacity was found to be 16.1 milliequivalents (m.e.) per 100 grams, and the exchange complex was almost completely saturated with calcium. The saturated soil *(21)*[2] (32.0 percent water) had a pH value of 7.76 and a specific conductance of 54×10^{-5} at 25° C. When the soil was allowed to come to equilibrium with 14.4 percent moisture and the soil solution was displaced in a pressure-membrane apparatus *(17, 18)*, this solution had a specific conductance of 102×10^{-5} mhos per centimeter at 25° and an osmotic pressure of 0.45 atmosphere, and the solutes were made up almost entirely of calcium chloride and bicarbonate. When the soil was moistened and allowed to come to equilibrium under a tension of 15 atmospheres in the pressure-membrane apparatus *(19)*, it retained 8.55 percent moisture. This corresponds fairly closely to the permanent wilting percentage of 9.2, as determined with sunflower plants. The normal moisture-holding capacity *(22)* was found to be 18.1 percent. The moisture sorption curve[3] of this soil is given in figure 1.

The experimental variables to be imposed upon this soil were as follows:

Salt treatment (all salt additions on dry-soil basis):	*Designation*
No added salt	0
0.1 percent added $NaCl$	C_1
0.2 percent added $NaCl$	C_2
0.4 percent added $NaCl$	C_4
0.2 percent added Na_2SO_4	S_2
0.4 percent added Na_2SO_4	S_4
0.8 percent added Na_2SO_4	S_8

The irrigation schedules were:

1. Soil irrigated with sufficient water to bring the moisture content to field capacity (approximately 20-percent moisture) when the average

[2] Italic numbers in parentheses refer to Literature Cited, p. 33.

[3] The writers are indebted to Milton Fireman, associate s... of this Bureau, for the data from which the curve was d...

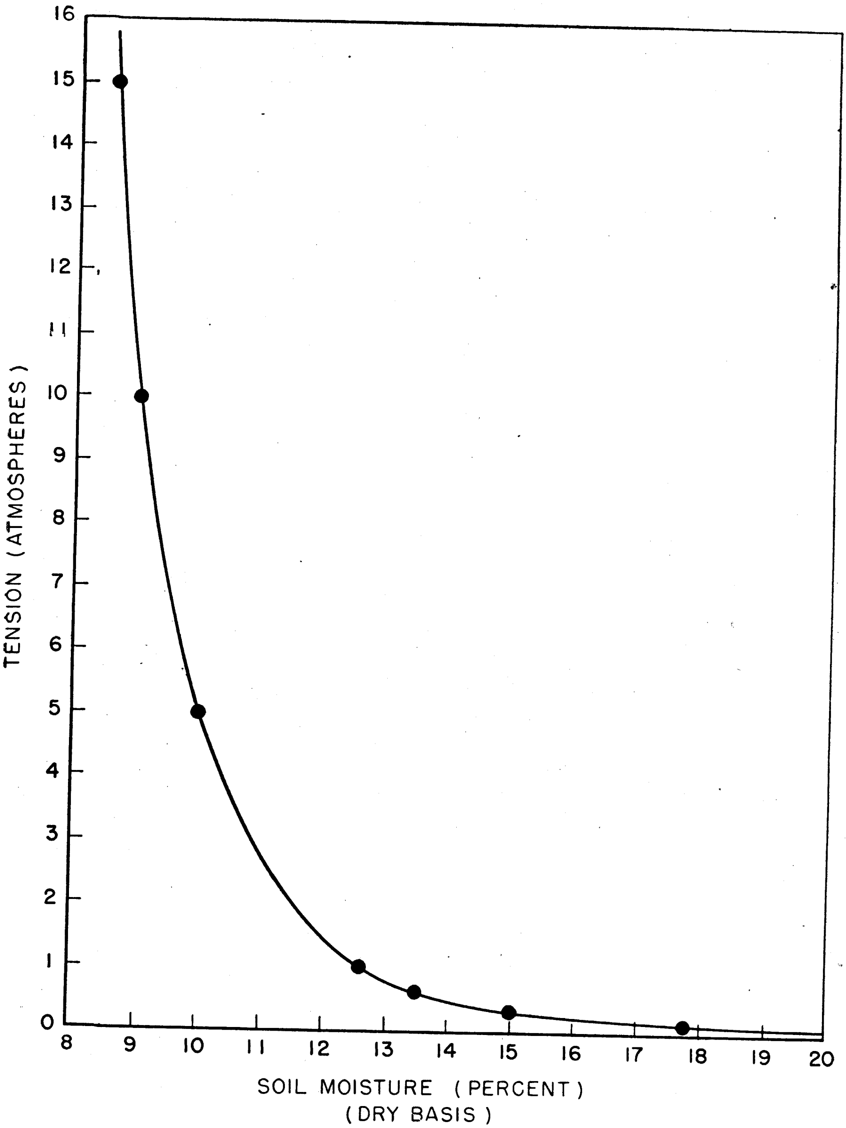

FIGURE 1.—Relation between moisture tension and moisture percentage in a sample of Panoche loam.

soil moisture obtained by weighing entire drum plus soil of a culture reached 14 percent. Tensiometers installed in certain soil cultures indicated the 14-percent soil moisture corresponded with a tension of 300 to 400 cm. of water at the 4-inch depth in the soil. This regime is designated by the letter L (low tension).

2. Soil irrigated with sufficient water to bring soil-moisture content to field capacity when average soil-moisture content of a culture reached 9 percent. This series is designated by the letter H (high tension).

3. Plants on irrigation schedule No. 1 for first part of experimental period (March 1 to July 9) and on irrigation schedule No. 2 for latter part of period (July 9 to December 1). This series is designated by letters L-H.

Each irrigation regime was applied in combination with each salt treatment, making 21 experimental variables. All treatments were thrice replicated. Steel drums with a 10-gallon capacity (adequate for 100 pounds of dry soil) were used as soil containers.

The proper quantity of salt for each treatment was mixed with the screened soil (1/4 inch) in a box suspended and rotated eccentrically. Besides the designated salt, 3 grams of 16-percent superphosphate and 85 grams of dry pulverized steer manure were added to each drum of soil. With the aid of a mechanical mixer and packer 106 pounds of the soil at a moisture content of 5 percent were placed in each container. The average volume weight of the soil in the drums so packed was found to be 1.28.

Before transplanting the plants to the drums, the soil-moisture content was brought to approximately the field capacity by the addition of 14 pounds of water to the surface of each drum of soil. This treatment leached the surface soil and caused an accumulation of the salt in the lower parts of the soil mass. For example, when 0.2 percent NaCl was mixed with this soil, the conductance of the extract of the saturated soil (32-percent moisture) was $1{,}290\times10^{-5}$ mhos per centimeter at 25° C. A drum of soil to which 0.2 percent NaCl was incorporated was sampled 5 days after the initial heavy application of water. The soil was segregated into three horizons, and the conductance of the extract of the saturated soil from each horizon determined. These conductance values in mhos per centimeter at 25° C. were (1) top horizon, 63.0×10^{-5}; (2) middle horizon, 129×10^{-5}; and (3) bottom horizon, $3{,}100\times10^{-5}$. Thus, salt accumulation in the bottom of the containers was even more pronounced at the beginning of the experiment than at the end.

Supplementary studies have indicated that a quasi-equilibrium in salt distribution within the containers was reached almost at the beginning of the experimental period as the result of the heavy initial irrigation and that the effect on salt movement downward of the lighter irrigations during the course of the experiment tended to be counteracted by salt movement upward during the irrigation interval. This supplementary evidence indicated that in most treatments the pattern of salt distribution was not greatly different at the end of the experiment from that following the initial heavy irrigation. This high degree of nonuniformity in salt distribution within the soil, however, suggested the necessity of developing a method *(26)* that would take this nonuniformity into account when evaluating the responses of the plants.

During the course of the experiment the soil was irrigated as required with Riverside tap water. The average analysis [4] of this water in equivalents per million is as follows: 1.43, Ca; 0.25,

[4] Furnished by courtesy of the Rubidoux Laboratory, Riverside, Calif.

Mg; 1.80, Na; 0.09, K; 0.72, Cl; 0.61, SO_4; and 2.22, HCO_3. All water was added to the surface of the soil.

The plants used in this study were obtained from the Alisal Nursery of the Emergency Rubber Project, Salinas, Calif. As received, they had taproots 20 to 25 cm. long and 3 to 5 mm. in diameter at the crown; the tops had been trimmed to 5 to 8 cm. in height. They were first embedded in sand and allowed to initiate a new flush of growth before plants were selected for study. On February 3, 1943, after the plants had been in the sand bed for about 5 weeks, 63 uniform plants were selected out of the original 200, and each was washed free of sand and transplanted to a drum of soil. After transplanting them the soil was washed in around the roots with 2 quarts of tap water, so that the rootlets would not immediately come into contact with saline soil.

During the course of the study the drums of soil were weighed every day to determine the average moisture content of the soil and when and what quantity of water should be applied. At each irrigation sufficient water was added to bring the average soil-moisture content to 20 percent.

On the first and fifteenth day of each month during the course of the study the maximum height and maximum width of each plant was measured. The product of these two measurements was taken as a growth index, in order to have a rough measurement of the rate of growth of each plant during the course of the study. These growth measurements were subjected to statistical analysis, and, although the findings lend added support to the interpretations here presented, it was decided to report the details of these growth-response curves elsewhere.

The plants were harvested on December 1, 1943, weighed, and air-dried in diffuse light. When the tops were dry, the leaves were stripped off and the stems and roots shipped to Raiford Holmes, of the Emergency Rubber Project, Salinas, Calif. The analyses for resin and rubber content were carried out under his direction.

After the plants had been harvested the soil in each drum was sampled. This involved dividing the 15-inch depth into three 5-inch horizons. The soil from each horizon was mixed, air-dried, and sampled for analysis. Observations as to depth and density of root penetration also were made at this time.

Each of the 189 soil samples was brought to the saturation percentage *(21)* with distilled water and allowed to stand over night, and the solution was extracted by placing the saturated soil on a Buchner funnel and applying suction. The specific conductance of each extract was determined. Certain extracts from selected treatments were subjected to complete inorganic analysis. Also, a part of the sample of soil from these selected treatments was adjusted to approximately 12-percent moisture and the soil solution displaced by means of the pressure-membrane apparatus *(17, 18)*. The specific conductance, osmotic pressure, and ionic composition of these solutions also were determined. The methods of chemical analysis suggested by Reitemeier *(15)* were followed.

RESULTS

Appearance of the Plants

At the termination of this experiment certain qualitative differences and similarities were noted in the appearances of plants grown under the different experimental conditions. Plants grown on soil with 0-added salt were in excellent condition regardless of soil-moisture regime. Even at the time of greatest depletion of soil moisture no evidence of wilting was observed.

Those grown on soil containing 0.1 percent NaCl were very similar in appearance to those with 0-added salt. Differences in soil-moisture regime in the presence of this quantity of salt likewise appeared to have few distinct qualitative effects upon the appearance of the plants.

When there was 0.2 percent NaCl in the soil the plants grown under a low moisture-tension regime appeared normal. Those that were shifted from the low to the high tension regime appeared to have a rather large proportion of their lower leaves dead or dying. Plants at this salt level that had been grown under the high moisture-tension regime appeared dead, or nearly so, since the major portion of their leaves had died.

Plants grown in the presence of 0.4 percent NaCl were just about normal when grown under the low soil-moisture-tension regime, with the exception that there appeared to be a somewhat abnormally high proportion of dead leaves at the base. Plants at this salt content of the soil that were shifted from the low to the high soil-moisture-tension regime were nearly dead at the time of harvest, only the whorl of leaves just below the terminal buds still showing green. Those grown on soil with 0.4 percent NaCl and continually maintained on the high soil-moisture-tension regime had died some 3 months before the termination of the experiment.

Plants grown in the presence of added Na_2SO_4 had a definitely different appearance from those grown in the presence of added NaCl. The leaves were a deeper bluish green and their glaucousness appeared to be more pronounced. With 0.2 percent added Na_2SO_4 the plants were remarkably similar to those in the control, "0-added salt" series; and even those with 0.4 percent added Na_2SO_4 were quite similar to the control plants, with the exception of the deeper bluish-green coloration of the leaves.

Plants grown with 0.8 percent added Na_2SO_4 were outstanding from those of other treatments in the unusually deep bluish green of the leaves and the appearance on them of an unusually pronounced development of glaucousness. This level of Na_2SO_4 did not induce an abnormal rate of dying of the lower leaves, as was the case in the presence of the highest level of NaCl. Differential soil-moisture regimes did not appear to be associated with qualitative differences among the plants grown on soil to which Na_2SO_4 had been added.

Quantitative Growth Responses

The average growth responses of the plants produced under the various experimental conditions are shown in table 1. Figure 2 presents the trends in growth response as measured by green

Table 1.—*Growth and rubber content of guayule under the various experimental conditions*

Treatment[1]	Green weight, tops	Millable bush	Resin	Rubber	Rubber per plant
	Gm.	*Gm.*	*Percent*	*Percent*	*Gm.*
OL	388	98.8	5.25	3.75	3.70
OH	283	62.1	5.88	6.24	3.87
OL–H	327	77.4	6.50	6.93	5.35
C_1L	353	84.4	6.31	5.62	4.74
C_1H	157	35.3	5.35	4.58	1.62
C_1L–H	257	58.6	6.21	5.73	3.35
C_2L	280	49.4	6.06	6.15	3.04
C_2H	79	12.1	5.36	3.62	.44
C_2L–H	172	38.6	6.38	5.12	1.97
C_4L	197	41.1	5.81	6.14	2.52
C_4H	10	0	0	0	0
C_4L–H	81	24.6	5.45	3.87	.95
S_2L	412	97.6	5.77	4.71	4.60
S_2H	288	62.5	5.77	6.57	4.11
S_2L–H	337	82.9	6.61	7.44	6.16
S_4L	397	86.0	5.25	4.69	4.03
S_4H	258	48.2	5.35	5.73	2.76
S_4L–H	277	53.7	5.46	5.90	3.17
S_8L	257	41.0	4.89	3.86	1.58
S_8H	140	22.7	4.94	5.09	1.15
S_8L–H	120	24.7	4.90	2.94	.73
Pooled standard error	3.61	[2] 2.24	[2] .12	[2] .18	[2] .18

[1] Abbreviations are explained on p. 2–4.

[2] Error term based on variability in cultures OL, OH, OL–H, C_1L, C_2L, S_2L, S_2H, S_2L–H, and S_4L.

weight of tops and as conditioned by level of soil salinity at the various soil-moisture regimes. Within a given salt level the smallest plants were those that were periodically subjected to high soil-moisture tension. Within each soil-moisture regime, increase in the concentration of NaCl in the soil was associated with a marked decrease in vegetative growth. These results parallel those previously reported for beans *(1, 27)*.

When Na_2SO_4 was added to the soil there was practically no decrease in vegetative growth until the added percentage of salt exceeded 0.4 percent. For a given soil-moisture regime even with the addition of 0.8 percent Na_2SO_4 the plants were definitely larger than those grown in soil having 0.4 percent added NaCl. The growth response in the Na_2SO_4 series indicates that the actual soil salinity was not nearly so high as that to be expected on the basis of the quantity of salt added to the soil. Data presented in a later section (pp. 15 to 23) will aid in explaining the results obtained for this series.

The plants were air-dried only, consequently the air-dry weights of the tops reported in table 2 include an undetermined quantity of imbibed water on the hydrophyllic colloids of the tissue. At the time this study was carried out the writers were advised that oven-drying the tissue had a detrimental effect on rubber content. The data presented in table 1 for millable bush include the dried stems and main roots of the plants. Since the trends for both dry weight of tops and millable bush almost coincide with those given in figure 2, for the green weight of tops, no further discussion of these two criteria of growth is necessary.

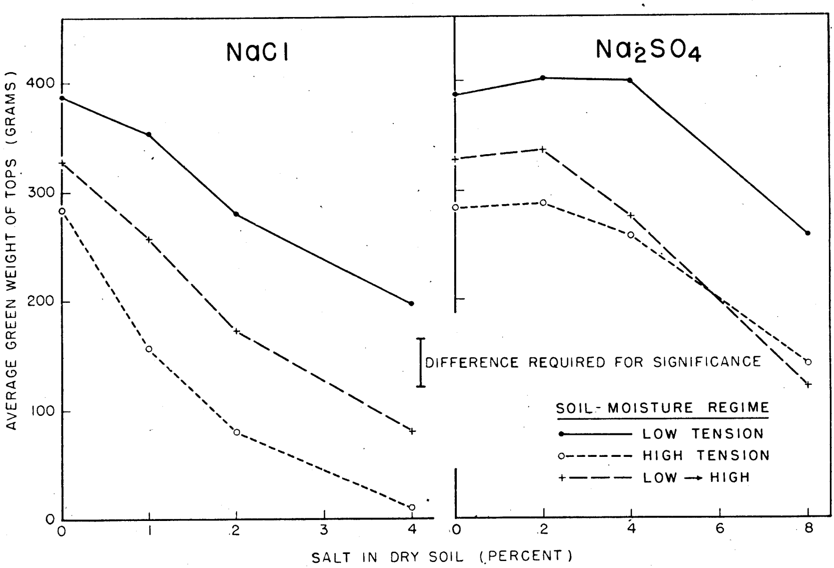

Figure 2.—Growth of plants under the various experimental conditions as measured by green weight of tops.

Rubber Accumulation

The percentages of resin and of rubber in the millable bush and the absolute quantity of rubber in grams produced per plant are also presented in table 1. The variations in percentage of resin appeared to be minor and as such merit little consideration in the present study. Variations in the percentage of rubber were rather marked and these are presented graphically in figure 3, *A;* as functions of the various experimental variables. Within the low-tension soil-moisture regime, 0.1, 0.2, and 0.4 percent NaCl in the soil resulted in a definite increase in percentage of rubber in the plants. This relationship tends to corroborate the view that a moisture stress to the plant (in this case, induced primarily by salt) is conducive to rubber formation. It is also evident that, in the absence of any added salt, when the soil-moisture tension is permitted to approach a high value prior to irrigation, as contrasted with maintenance at a low level, a marked increase in rubber accumulation resulted. This is in agreement with the findings of Kelley and associates *(12).*

In the moisture series that were subjected to periods of high moisture tension or were shifted to this regime during the latter

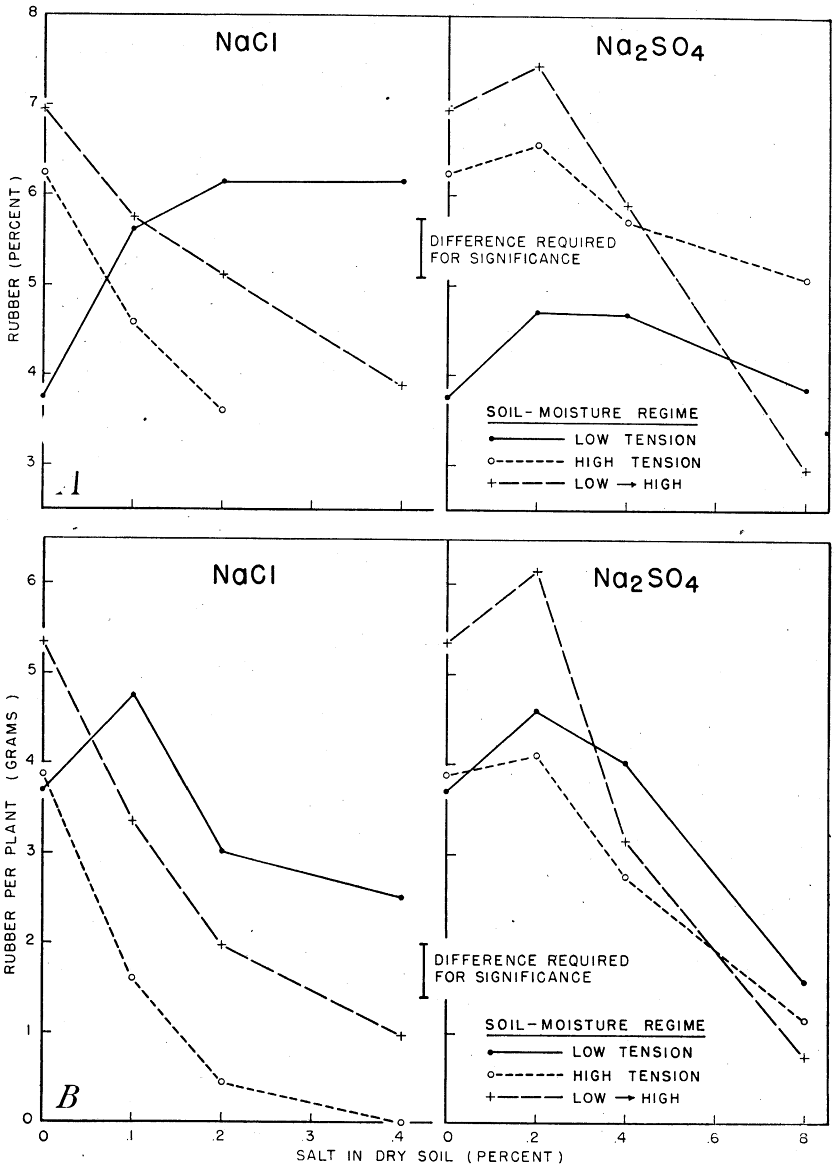

FIGURE 3.—*A*, Percentage of rubber in the millable bush; *B*, absolute quantity of rubber produced per plant under the various treatments.

part of the growing season, however, the presence of NaCl in the soil had a deleterious effect on rubber accumulation. Since rubber is a derivative of the photosynthate of the plant, it is to be expected that any condition that might impair photosynthesis or the accumulation of the products of photosynthesis would affect rubber accumulation. High concentrations of the chloride ion in the substrate have been found detrimental to sugar formation

TABLE 2.—*Water utilization by guayule under the various treatments*

Treatment [1]	Air-dry weight of tops	Water applied per plant	Water per gram of —		
			Air-dry weight of tops	Millable bush (stem plus main root)	Rubber
	Grams	*Liters*	*Liters*	*Liters*	*Liters*
OL	201.0	303	1.51	3.07	82.0
OH	136.5	189	1.38	3.04	48.6
OL-H	161.0	238	1.48	3.08	44.5
C_1L	174.1	279	1.60	3.30	58.8
C_1H	80.3	112	1.40	3.17	69.2
C_1L-H	132.2	193	1.46	3.30	57.6
C_2L	136.1	206	1.51	4.17	67.7
C_2H	33.4	63	1.89	5.20	143.0
C_2L-H	89.4	136	1.52	3.52	69.1
C_4L	92.2	165	1.79	4.02	65.5
C_4H	8.2	28	3.42	....	....
C_4L-H	59.7	98	1.64	3.98	103
S_2L	191.3	314	1.64	3.22	68.3
S_2H	135.1	181	1.34	2.90	44.0
S_2L-H	163.9	234	1.43	2.82	38.0
S_4L	179.5	293	1.63	3.41	72.6
S_4H	114.8	165	1.44	3.43	59.8
S_4L-H	125.2	204	1.63	3.80	64.4
S_8L	106.2	194	1.83	4.73	123.0
S_8H	60.0	105	1.75	4.63	91.4
S_8L-H	60.0	112	1.87	4.53	153.0
Standard error	1.42	1.25	.021	.049	[2] 2.26

[1] Abbreviations are explained on p. 2-4.
[2] Error term based on variability in cultures OL, OH, OL-H, C_1L, C_2L, S_2H, S_2L-H, and S_4L.

and starch accumulation in the potato plant *(2, 3)*, and there is some evidence that high concentrations of NaCl in the soil solution adversely affect the carbohydrate metabolism of the bean plant *(27)*. If the chloride ion has this effect upon the photosynthetic activity of the guayule plant the observed trends in rubber accumulation for the high soil-moisture-tension plants as affected by NaCl are within expectation.

This, however, would not account for the apparent accumulation of rubber in the presence of added NaCl in the low soil-moisture-tension regime. It was previously noted that plants periodically subjected to high soil-moisture tensions and high levels of NaCl showed an inordinate degree of dying of the lower leaves. This abnormal lowering in the photosynthetic surface of the plant may account for the lower rubber production in plants subjected to the high concentrations of NaCl when the soil-moisture regime involved high tension.

When Na_2SO_4 was added to the soil the effect on rubber accumulation showed somewhat different trends from those observed in the NaCl series. Thus, in the low moisture-tension series added Na_2SO_4 had little if any significant effect on rubber accumulation as compared with the control, 0-added salt, plants. Within each respective salt level, subjecting the plants to a high moisture-tension regime resulted in a significant increase in percentage of rubber with the exception of the plants grown with 0.8 percent added Na_2SO_4 and shifted from the low to the high tension-moisture regime. This latter anomalous observation may be an analytical error. It certainly cannot be readily explained on the basis of the data available.

From an economic standpoint the yield of rubber per acre is a function of both vegetative growth and rubber percentage. The present data may be evaluated in terms indicative of the rubber production per unit area by reference to figure 3, *B*, showing the relationship between grams of rubber accumulated per plant and the various experimental variables. In the NaCl series, with the exception of the plants grown in 0-added salt at low soil-moisture tension, the periodic subjection of plants to the high moisture tension lowered the rubber yield, as did also increasing the salt content of the soil. The seemingly anomalous position of the aforementioned plants on treatment OL was due to the relatively low percentage of rubber in these plants. In the Na_2SO_4 series it is evident that, for the most part, an increase in the salinity of the soil is associated with a decrease in rubber production, with the exception that the control series tended to produce plants with a lower absolute quantity of rubber than those grown on soil containing 0.2 percent Na_2SO_4. The soil-moisture regimes appeared to have little distinct effect in the Na_2SO_4 series, except that in the 0-added and 0.2-percent-added Na_2SO_4 series the plants shifting from low to high soil-moisture tension gave the highest quantities of rubber per plant of any in the experiment.

WATER REQUIREMENT

Since much of the guayule now being grown is produced under irrigation, it is expedient to consider the water economy of this plant. The average quantity of water supplied to each plant during the experimental period, together with the ratios of the quantity of water added to dry-matter accumulation and to rubber production, are presented in table 2. The applications of water per plant, as conditioned by treatment, follow the same general trends as the ones shown in figure 2 for growth response, i.e., the larger the plants the more water applied to the culture.

There were certain differences, however, in the ratio of dry matter produced in the plants per given quantity of water applied. With the exception of the C_4H plants that died, 1.4 to 2.0 liters of irrigation water were applied during the experimental period for each gram of dry weight of tops produced. The efficiency of water utilization tended to be higher under the irrigation regimes involving high soil-moisture tension prior to irrigation. The data on water utilization perhaps have a more practical bearing if considered on the basis of liters of water applied per gram of millable bush produced. The trends for these data are shown in figure 4, *A*. This indicates that in the presence of 0-added salt slightly less water was needed to produce a gram of millable bush under high than under low moisture-tension regimes, but the difference is not significant. In terms of production of millable bush the main point that these data bring out is that an increase in salt concentration of the soil is associated with a decrease in efficiency of water utilization.

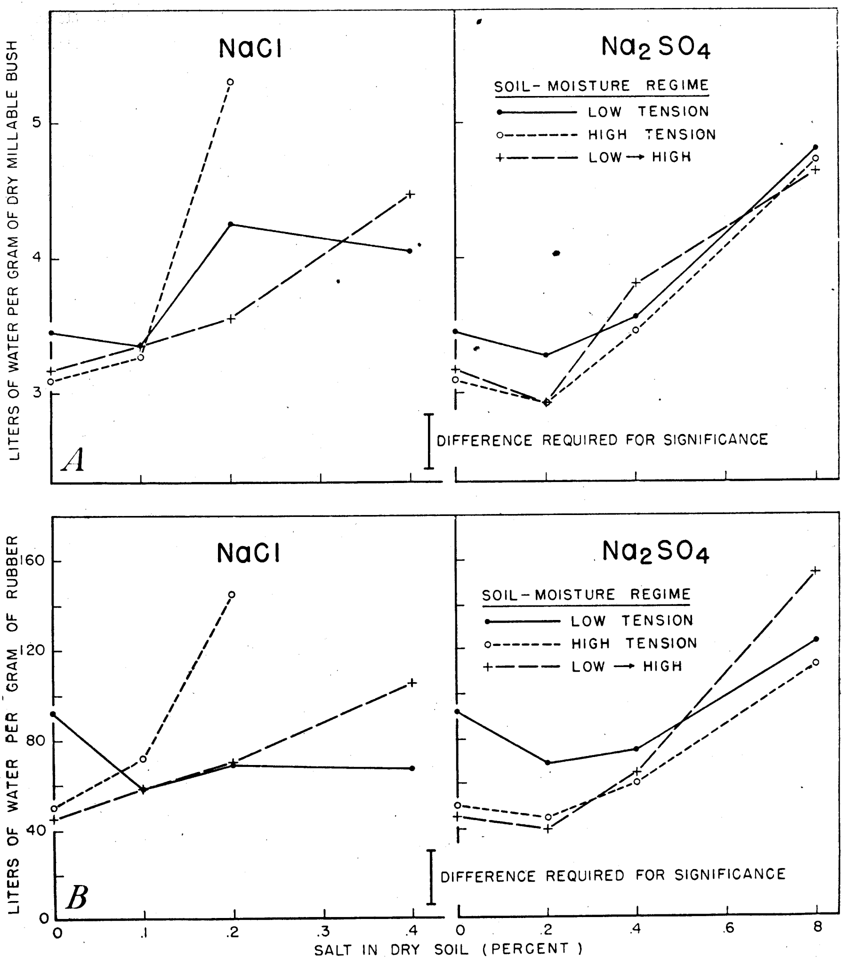

FIGURE 4.—Quantity of water applied (*A*) per gram of millable bush and (*B*) in terms of grams of rubber produced by the various treatments.

The ratio of water application to grams of rubber produced is shown in figure 4, *B*. It is evident that plants periodically subjected to high moisture tension had a significantly higher efficiency of rubber production in terms of water application than those grown continually under the low moisture-tension regime. This differential, however, disappeared in the presence of added salts. In the main, the efficiency of rubber production in terms of water application tended to decrease with an increase in soil salinity. The main exception to this was that under low soil-moisture tension a small quantity of salt present in the soil tended to bring about an increase in the efficiency of rubber production per given quantity of water applied. These data would indicate that where cost of irrigation water is a significant contributor to cost of production, the presence of saline soil would tend to enhance considerably the cost of rubber production. For example, under some treatments more than three times as much water is required to produce a gram of rubber as in others.

CONDUCTANCE OF THE SOIL EXTRACTS

In the preceding presentation the observations have been considered on the basis of percentage of salt actually mixed with the soil. This criterion of classification, however, has two outstanding weaknesses: (1) As a result of adding water to the surface only it is obvious that the salt added to the soil would not maintain its original uniform distribution but would tend to be leached towards the lower horizons *(1)*; (2) the decrease in activity of the soil water induced by dissolved solids would not be directly related to the quantity of salt added to the soil but would be conditioned by reactions between the salt added and the chemical components of the soil itself. The direction and degree of salt movement are shown in figure 5.

As a general rule the salt content was lowest in the surface horizon of soil in the drums and highest in the deepest horizon. The exceptions to this were that in the H and L-H series of soil-moisture treatments with 0.4 percent NaCl the salt content of the soil solution at the surface horizon was as high as in the lower horizons or higher. This exceptional observation was related to the early death of the plants and the consequent cessation of irrigation, which resulted in the salts migrating surfaceward by capillarity and accumulating because of surface evaporation.

Theoretically, 2 grams of Na_2SO_4 dissolved in a given quantity of water should give rise to a slightly lower activity of the solvent than when 1 gram of NaCl is added to the same quantity of water. The conductances of the extracts of the saturated soil (fig. 5) show that this theoretical relationship was altered when these respective salts were added to this Panoche soil. Additions of Na_2SO_4 did not have a directly commensurate effect on the lowering of the activity of the soil moisture. It is especially remarkable that in the surface horizon the addition of Na_2SO_4 had very little effect upon the conductance of the soil extract, unless more than 0.4 percent of this salt was originally present. This finding is related to the observations presented in figure 2, showing that unless the soil initially contained more than 0.4 percent Na_2SO_4 there was little if any effect upon growth of guayule. These data also suggest that, especially within the low moisture-tension regime, the salt concentration of the surface horizon (5 inches) of soil was the main one affecting growth. Such a correlation would be in agreement with the observations of Eaton *(6)* and Long *(13)* that roots of plants remove water mainly from the part of the substrate that has the lower osmotic pressure.

This relation between the conductance of the extract from the surface horizon of the soil and the growth of the plant is shown in figure 6. It may be seen that within a given soil-moisture-tension regime, growth approaches a nearly linear relationship with the logarithm of the conductance of the soil extract of the surface horizon. It is also evident that modifications in the soil-moisture

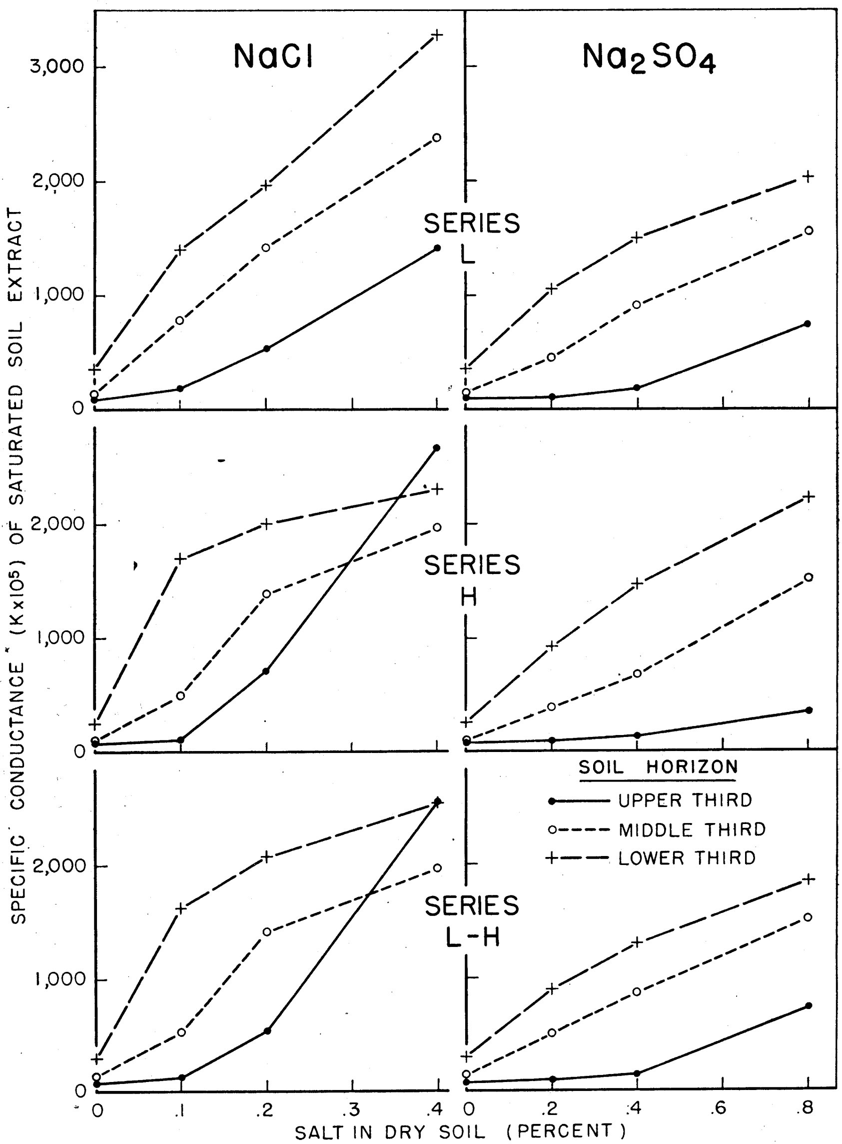

FIGURE 5.—Specific conductance of the extract of the saturated soil found at the termination of the experiment for the different treatments.

regime cause a definite displacement in plant response to salinity, with the result that plants subjected to a high soil-moisture tension made consistently poorer growth than those of corresponding salt treatments subjected only to low soil-moisture tension.

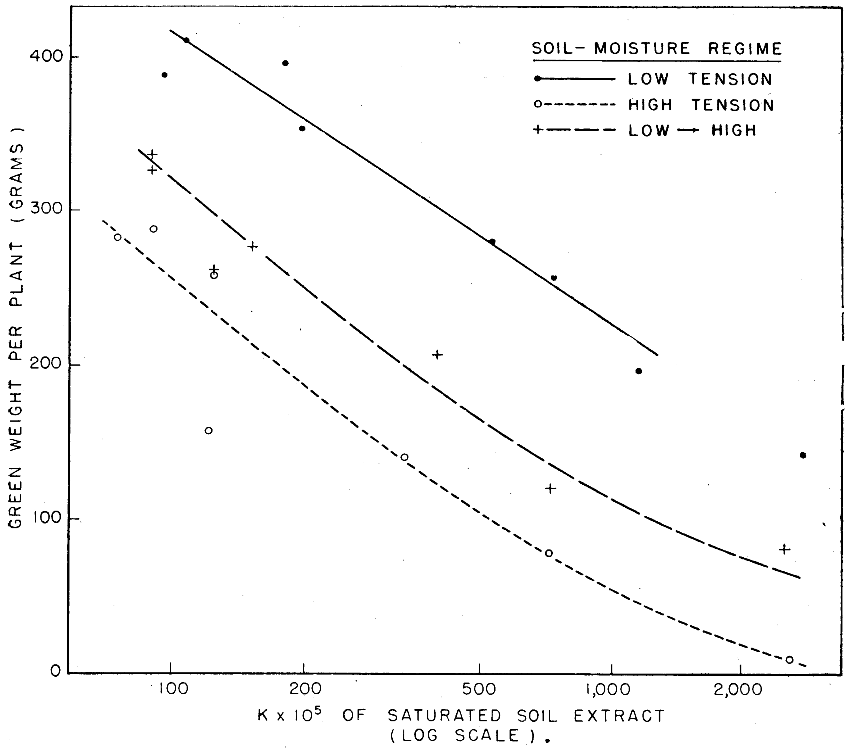

FIGURE 6.—Relation between growth of plants and specific conductance of the extract of the saturated soil from the surface horizon.

CONCENTRATION OF SOIL SOLUTIONS

The foregoing data on conductance of the soil extract were based on the soil-moisture percentage at saturation. Depending on the types of soil and salts present, it is known that the qualitative composition of the soil solution will change with moisture percentage *(7, 16)*. Although it was expedient to make conductance determinations on the extract of the saturated soil on all 189 samples, it would not have been feasible to extract this number of samples at a low moisture content by use of the pressure-membrane apparatus. It did seem advisable, however, to evaluate the relation between the conductance of the soil solution at the saturation percentage and the conductance of the soil solution within the field-moisture range.

As shown in table 3 the soil solution of certain selected samples was removed by means of the pressure-membrane apparatus at a moisture content of approximately 11 to 12 percent and the conductance of the solution determined. The relation between the conductance of the soil extract made at the saturation percentage and that of the soil solution obtained at 12 percent soil moisture is shown in figure 7, *A*. It is evident that the relationship for soil to which NaCl was added is different from soil that received Na_2SO_4. It is to be recalled that Panoche loam soil is almost saturated with calcium. When Na_2SO_4 was added to this calcium-saturated soil, sodium entered the exchange complex, liberating calcium, and gypsum ($CaSO_4 2H_2O$) was formed.

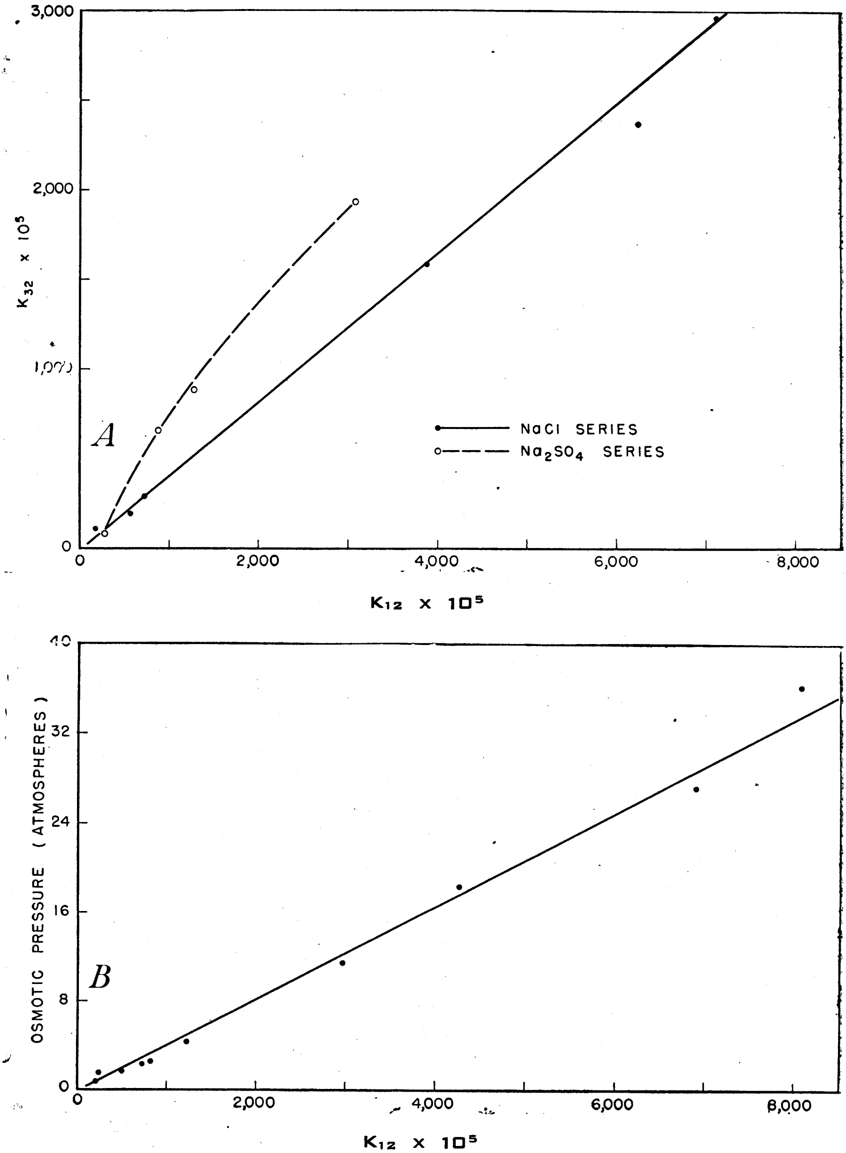

FIGURE 7.—Observed relations between (*A*) the specific conductance of the extract of the saturated soil (32 percent H_2O) and that of the soil solution (12 percent H_2O) and (*B*) the specific conductance and the osmotic pressure of the soil solution.

It appears that the variation in the quantity of $CaSO_4$ in solution *(16, 24)* at different percentages of soil moisture is involved in soils at which Na_2SO_4 has been added. The relationships in figure 7, *A*, present a rather satisfactory basis for conversion of the conductance made at the saturation percentage to conductance of the soil solution at 12 percent moisture, which is within the field-moisture range. The cryoscopically determined osmotic pressure of the soil solutions at 12 percent soil moisture and also the osmotic pressure of the soil solutions that might be expected at different soil-moisture percentages are shown in table 3. The relation between the conductance of the solution and its osmotic pressure is shown in figure 7, *B*. This regression was found by the method of least squares to be 255×10^{-5} mhos per atmosphere. Thus it is possible to convert the conductances presented in figure 6 for the soil extract at the saturation percentage to osmotic pressures of the soil solution at various percentages within the field-moisture range.

TABLE 3.—*Specific conductance and osmotic pressure of soil solutions*

Treatment	Horizon (in thirds)	H_2O as extracted	$K \times 10^5$ at 25° C.	Osmotic pressure	$K \times 10^5$ calculated at 12 percent H_2O	Osmotic pressure calculated at — 9 percent	12 percent	15 percent	18 percent
		Percent		*Atmospheres*		*Atmospheres*	*Atmospheres*	*Atmospheres*	*Atmospheres*
OL-H	Upper	10.62	211	0.78	187	0.92	0.69	0.55	0.46
	Lower	11.17	736	2.37	685	2.94	2.21	1.76	1.47
C_1L-H	Upper	11.15	507	1.71	472	2.12	1.59	1.27	1.06
	Lower	10.88	4,250	18.46	3,910	22.3	16.7	13.4	11.2
C_4L-H	Upper	10.58	8,090	36.28	7,130	42.7	32.0	25.6	21.4
	Lower	10.87	6,910	27.14	6,250	32.8	24.6	19.7	16.4
S_2L-H	Upper	11.63	235	1.65	228	2.13	1.60	1.28	1.07
	Lower	12.53	1,230	4.47	1,290	6.22	4.67	3.74	3.11
S_8L-H	Upper	12.64	821	2.55	865	3.58	2.69	2.15	1.79
	Lower	12.53	2,960	11.42	3,090	15.9	11.95	9.55	7.25

The values for osmotic pressure given in table 3 include, in addition to those for the actual solution from the pressure-membrane apparatus, those calculated for the soil solution if the soil moisture had been at 9, 12, 15, or 18 percent. Even at a high moisture content the osmotic pressure of the soil solution in the presence of 0.4 percent NaCl would have been prohibitive to growth of most plants. It is certain that the guayule in cultures C_4L-H did not make the little growth they did in substrates having an osmotic pressure of the substrate of more than 20 atmospheres. These cultures undoubtedly had a relatively low salt concentration in the surface horizon during the early part of the season. This is indicated by data of Ayers and others *(1)*, obtained under comparable experimental conditions. After the shift in soil-moisture regime, these plants made little growth and consequently required little water. This extended period without irrigation during the latter part of the experiment permitted the salt to migrate to the surface horizon, owing to evaporation from the soil surface.

For each respective increment in salt addition, NaCl resulted in much higher values for the osmotic pressure of the soil solution than did Na_2SO_4.

Ionic Composition of Soil Extracts and Soil Solutions

The type of data presented in figure 5 and table 3 suggested the advisability of determining the ionic composition of certain of the soil extracts and solutions. Data for the ionic composition of the saturated soil extract for each horizon of soil for one replicate of the L-H series are given in table 4. The relationships involved are partially shown in figure 8. The striking feature of

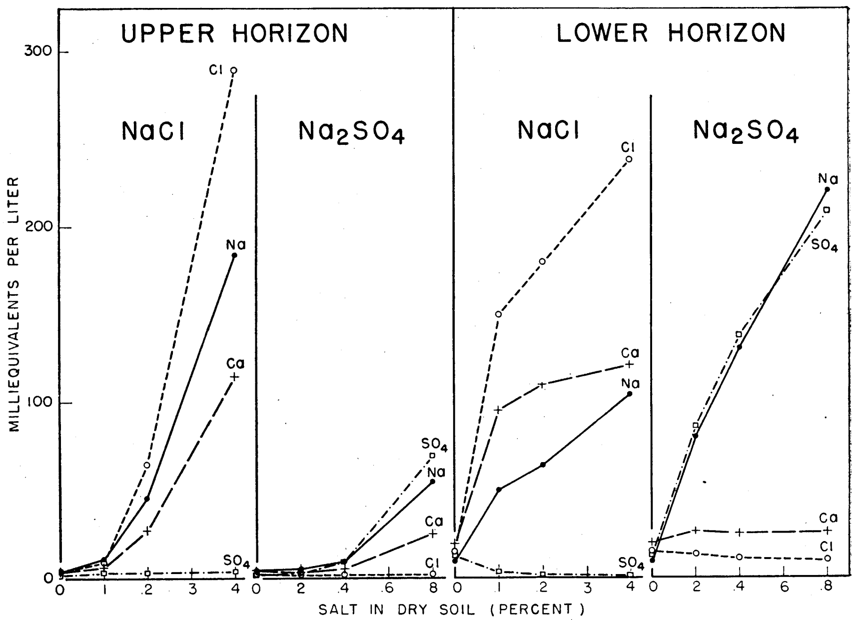

FIGURE 8.—Composition of the extract of saturated soil from the upper and lower horizons in the soil containers.

these data is the very high values found for soluble calcium and magnesium in the cultures receiving NaCl as compared with those receiving Na_2SO_4. With reference to culture C_4L-H the soluble calcium greatly exceeded the quantity added in the tap water, indicating that most of this calcium was either displaced from the exchange complex or derived from the $CaCO_3$ present in the original soil. The comparatively low values for Ca in the sulfate cultures is due to the low solubility of $CaSO_4$. That is, the sulfate ion is present in excess in the sulfate cultures and the solubility of Ca will be largely determined by the solubility product and ionic strength phenomena *(24)*.

The ionic composition of the soil solutions adjusted to a 12-percent soil moisture is shown in table 5. Also, respective calculated values derived from the ionic composition of the saturated soil extract are given in table 4. In making this adjustment, simple concentration of the components was assumed. It is obvious that some of the calculated values for calcium would be impossible in the presence of the designated quantity of sulfate.

Within the cultures receiving added NaCl the concentration of sodium in the soil solution was only a fraction of the concentration of chloride, even though these two ions were added in equivalent quantities. This means that a considerable proportion of the added sodium displaced the calcium and magnesium from the exchange complex, bringing about the relatively high concentrations of the latter two ions in the soil solution.

TABLE 4.—*Analyses of saturated soil extracts*

[E. p. m. (equivalent per million) at 32 percent moisture]

Drum No.	Treatment	Horizon (in thirds)	Ca	Mg	Na	Cl	SO_4	HCO_3	CO_3	Total cations	Total anions
			E. p. m.	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*
51	OL-H	Upper	4.14	0.88	4.02	3.08	2.19	3	....	9.04	8.27
		Middle	3.73	.76	8.01	4.21	4.27	2.63	0.13	12.5	11.2
		Lower	19.2	2.94	9.01	14.5	12.7	1.90	.11	31.1	29.2
58	C_1L-H	Upper	6.50	.77	11.1	9.25	3.57	3.16	.47	18.4	16.4
		Middle	16.6	2.26	38.9	47.1	6.53	2.57	.21	57.8	56.4
		Lower	94.7	14.5	49.9	149	3.48	1.66	.08	159	154
118	C_2L-H	Upper	27.7	4.15	46.2	65.5	3.21	1.97	....	78.1	70.7
		Middle	48.6	7.86	77	118	3.83	1.75	....	133	123
		Lower	110	22	64	180	1.94	1.84	....	196	184
44	C_4L-H	Upper	115	18.3	185	291	4.13	1.73	....	318	297
		Middle	58.1	6.82	104	161	1.85	2.13	....	169	165
		Lower	122	24.3	104	238	1.53	2.11	....	250	242
73	S_2L-H	Upper	3.21	.52	4.90	1.90	2.39	3.98	....	8.63	8.27
		Middle	16	2.41	32.4	4.57	39.7	3.64	....	50.8	47.9
		Lower	26.5	5.20	80	13.4	86.2	5.14	....	112	105
102	S_4L-H	Upper	5.06	.29	9.69	1.93	9.42	3.82	....	15	15.2
		Middle	26.4	3.78	75.4	5.65	92.1	3.84	....	106	102
		Lower	25.5	5.83	131	11.6	139	5.82	....	162	156
98	S_8L-H	Upper	25.2	1.59	54.8	2.07	69.7	3.98	.14	81.6	75.9
		Middle	24.9	6.14	176	6.08	182	3.78	.80	207	193
		Lower	26.4	8.87	222	10.3	209	5.07	.72	257	225
Original soil	......	....	3.82	.52	.48	.74	.41	2.66	.26	4.82	4.07

It is to be noted that the concentration of chloride in the soil solution is consistently higher than that calculated from the concentration in the extract of the saturated soil. Eaton and Sokoloff *(7)* and Reitemeier *(16)* have previously observed this phenomenon. It has been explained that the initial layers of water about the colloidal particles are held by a relatively high force. The water thus "bound" undergoes a reduction in solvent power *(5)*, causing a relative increase in the solute concentration of the "unbound" water. Obviously, the lower the moisture content of the soil at which the soil solution is removed, the greater the proportion of water that is bound and the greater the modification of this effect on concentration of solute. Reitemeier *(16)* suggests that negative adsorption of monovalent anions may be involved in this phenomenon.

Comparable data on the quantities of salt actually added to various drums of soil, inclusive of that added by the irrigation water, and on the quantities found in the extract of the saturated soil at the end of the experiment are given in table 6. It is obvious that the irrigation water added considerably more salt to the soil of the OL-H treatment than could be found in the soil solutions at the end of the experiment. Disappearance of the HCO_3 could be accounted for on the basis of CO_2 evolution or $CaCO_3$ precipitation. The precipitation would also account for the disappearance of the calcium. There is undoubtedly a moderate degree of error in the comparative figures, which accounts for the discrepancy in the values for chloride and sulfate. The large difference in the quantity of sodium added in the irrigation water and that found in the soil extract is the most remarkable characteristic of the data in this table, not only for the OL-H series but for all the salt treatments.

TABLE 5.—*Comparison between the ionic composition of soil solutions and of saturated soil extracts, both calculated to 12 percent soil moisture*

Drum No.	Treatment	Horizon (in thirds)	Solution	Ca	Mg	Na	Cl	SO_4	HCO_3	Total cations	Total anions
				E. p. m.	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*	*E. p. m.*
51	OL-H	Upper	Soil soln.	9.29	1.60	11.0	10.2	2.06	2.48	21.9	14.7
			Satn. ext.	11.0	2.35	12.8	8.21	5.84	8.00	26.1	22.0
		Lower	Soil soln.	50.2	7.71	21.3	48.9	21.2	3.16	79.2	73.3
			Satn. ext.	51.2	7.84	24.0	38.6	33.9	5.07	83.0	77.6
8	C_1L-H	Upper	Soil soln.	20.7	2.95	21.7	30.8	7.16	2.28	45.3	40.2
			Satn. ext.	17.3	2.05	29.7	24.7	9.52	8.43	49.0	42.6
		Lower	Soil soln.	333	54.1	115	494	6.33	2.72	502	503
			Satn. ext.	252	38.6	133	398	9.28	4.43	424	412
44	C_4L-H	Upper	Soil soln.	399	55.1	429	838	3.66	1.76	883	843
			Satn. ext.	306	48.8	492	775	11.0	4.61	846	791
		Lower	Soil soln.	404	58.4	240	702	1.85	2.26	702	706
			Satn. ext.	324	64.9	277	635	4.08	5.63	666	645
73	S_2L-H	Upper	Soil soln.	9.38	1.58	10.3	12.6	4.46	2.04	21.3	19.1
			Satn. ext.	8.56	1.39	13.1	5.07	6.37	10.6	23.0	22.0
		Lower	Soil soln.	28.0	6.27	117	51.4	88.4	8.14	151	148
			Satn. ext.	70.7	13.9	213	35.7	230	13.7	298	279
98	S_8L-H	Upper	Soil soln.	25.0	3.21	71.1	10.0	72.5	3.90	99.3	86.4
			Satn. ext.	67.1	4.24	146	5.52	186	10.6	217	202
		Lower	Soil soln.	22.2	16.1	377	36.0	308	9.71	415	354
			Satn. ext.	70.5	23.6	592	27.4	557	13.5	686	598

The explanation of this large disappearance of added sodium may be partly found in the phenomenon of exchange equilibrium. The Gapon equation *(9, 14)* has been found applicable to the equilibrium between the ratio of sodium and calcium ions in the soil solution and the ratio of these cations on the exchange complex. Thus,

$$\sqrt{\frac{[Ca^{++} + Mg^{++}]}{[Na^{+}]}} \times \frac{NaX}{CaX} = K$$

where $[Ca^{++} + Mg^{++}]$ and $[Na^{+}]$ are the millimolar concentrations of these ions in the soil solution and NaX and CaX represent the milliequivalents of these cations adsorbed per 100 gm. of dry soil. In the sample of Panoche loam studied, the equilibrium constant (K) was found to be 0.015. Using the previously mentioned base exchange capacity of this soil, 16.1 m.e. per 100 gm., it was possible to calculate the average quantity of exchangeable sodium on the complex for each horizon of these seven salt treatments by the following rearrangement of the equation above to—

$$NaX = \frac{0.015 \quad [Na^{+}] \quad 16.1}{\sqrt{[Ca^{++} + Mg^{++}]} + 0.015\ Na^{+}}$$

The average percentage of sodium on the exchange complex for each drum of soil was also calculated. There were 7,300 m.e. of exchange capacity to each 100 pounds of soil in a container, and the original soil was found to have 0.5 percent exchangeable sodium. The comparison between the quantities of sodium calculated to have gone into the exchange complex on the basis of the Gapon equation and the difference between the quantity of sodium added and that found in the soil extract are shown in table 7. Considering the limitations of the methodology the agreement is remarkably close. This is especially true if one considers that the presence of gypsum and calcium carbonate in a soil have an undetermined effect upon the equilibrium relationship as expressed by the Gapon equation.[5]

TABLE 6.—*Quantities of various ions added to a drum of soil, as compared with quantities found in the soil solution*

Treatment	Ca		Mg		Na		HCO_3	
	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]
	M. e.	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*
OL–H	343	131	60	22	432	101	533	36
C_1L–H	272	570	48	85	1,120	482	422	35
C_2L–H	185	900	32	165	1,790	906	286	27
C_4L–H	136	1,420	25	240	3,290	1,890	211	29
S_2L–H	345	221	60	39	1,710	570	535	61
S_4L–H	296	276	52	48	2,930	1,040	460	65
S_8L–H	172	370	30	81	5,320	2,180	266	62

Treatment	Cl		SO_4		Total cations		Total anions	
	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]
	M. e.	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*
OL–H	173	105	146	92	835	254	852	233
C_1L–H	914	993	116	65	1,440	1,140	1,450	1,090
C_2L–H	1,650	1,760	79	43	2,000	1,970	2,010	1,830
C_4L–H	3,180	3,340	58	36	3,450	3,550	3,450	3,400
S_2L–H	174	96	1,430	620	2,120	830	2,140	777
S_4L–H	149	93	2,680	1,160	3,270	1,360	3,290	1,320
S_8L–H	86	89	5,170	2,220	5,520	2,630	5,520	2,370

[1] From tap-water additions plus originally added salt.

[2] Based on extract of saturated soil.

The data in tables 6 and 7 emphasize the modifications that took place in the soil complex as a result of the imposed treatments. Three major modifications are in evidence: (1) Although sodium was the main cation added to the soil solution, the soil solution or extract at equilibrium may be high in calcium (chloride series); (2) the total concentration of the soil solution or extract may be much less than might be expected on the basis of

[5] Private communication from Milton Fireman, of this Bureau.

the quantity of soluble salt added ($CaSO_4$ precipitation in SO_4 series); (3) the percentage of sodium on the exchange complex may become sufficiently high—10 to 15 percent *(23)*—to impose a detrimental effect on the soil structure.

TABLE 7.—*Relationship between disappearance of added sodium from the soil solution and increase in sodium on the exchange complex*

Treatment	Average Na on exchange complex	Increase in exchangeable Na per 100 pounds of soil	Difference between added and found Na (table 6) per 100 pounds of soil
	Percent	*Millequivalents*	*Millequivalents*
OL-H	5.0	328	331
C_1L-H	11.1	775	738
C_2L-H	14.4	1,050	884
C_4L-H	21.1	1,500	1,400
S_2L-H	14.0	990	1,140
S_4L-H	21.3	1,520	1,890
S_8L-H	34.3	2,470	3,140

The modifications in the soil complex affected by the salt added cannot be ignored in the interpretation of the plant responses. Interpretation was further complicated, however, by variability in salt distribution within a drum of soil, as illustrated by table 8. This table indicates what the concentration of chloride and sulfate would have been in the soil solution at the 12-percent moisture value if all these added ions had remained in solution and had been uniformly distributed within the soil solution of the different horizons. The data in table 8 were derived from tables 4 and 5. Values not found in table 5 for the 12-percent moisture value were calculated with the aid of the relation between comparable values determined at both 32- and the 12-percent moisture values. Table 8 shows that there would have been 165 e. p. m. of chloride in the soil solution (C_1) if all added chloride was uniformly distributed in the soil solution at 12-percent moisture. It was observed in sand-culture studies that 100 e. p. m. of chloride were highly inhibitive to the growth of guayule *(28)*.

In the present study, plants made very satisfactory growth in treatments receiving 0.1 percent NaCl and 0.2 and 0.4 percent Na_2SO_4. It is evident, therefore, that the relatively low concentrations of salt in the surface horizon (table 8), due to leaching or chemical reaction, were highly important in permitting the good growth of guayule observed in these cultures. The values for chloride found in the surface horizon of the C_2L-H and C_4L-H treatments are undoubtedly abnormally high in view of the extent of growth observed, especially in the series of plants continuously on a low-tension soil-moisture regime. That is, these determinations were made after an appreciable interval following the final irrigation. During this time salts would move back into the surface horizon that had been leached out at the time of irrigation. It appears that the average percentage of salt in the root zone of a plant may not be an adequate criterion on which to interpret plant response to a saline soil.

TABLE 8.—*Distribution of the soluble chloride and sulfate among three horizons*

Treatment	Upper third				Middle third				Lower third			
	Cl		SO_4		Cl		SO_4		Cl		SO_4	
	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]	Added [1]	Found [2]
	M. e.	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*	*M. e.*
OL	31	10.2	26	2.06	31	14.0	26	6.2	31	48.9	26	21.2
C_1L-H	165	30.8	21	7.16	165	156	21	12.0	165	494	21	6.3
C_2L-H	297	203	14	5.40	297	353	14	6.5	297	560	14	3.9
C_4L-H	573	838	10	3.66	573	475	10	2.0	573	702	10	1.85
C_2L-H	31	12.6	256	4.46	31	23	256	42.0	31	51.4	256	88.4
S_4L-H	27	11.0	484	13.0	27	27	484	120	27	43.0	484	180
S_8L-H	16	10.0	932	72.6	16	24	932	250	16	36.0	932	308

[1] From tap-water additions plus originally added salt.
[2] Based on extract of saturated soil.

DISCUSSION

The foregoing data emphasize the inadequacy of evaluating plant response entirely on the basis of the quantities of a constituent added to a soil as compared with a consideration of the resultant status of the soil complex and soil solution following the incorporation of the added constituent. This is particularly the case in studies involving experimentally induced soil salinity. On addition of a salt that changes both the quantitative and qualitative content of dissolved cations in the soil solution the equilibrium distribution of the adsorbed ions and those in the soil solution will be shifted. Thus, the status of the whole soil in the various treatments of this experiment was something quite different from what might be expected from merely dissolving a specified quantity of a given salt in a volume of water equivalent to that present in the designated mass of soil.

That it would be fallacious to interpret the observed plant responses as being conditioned by a given percentage of salt in the soil mass is obvious from the foregoing. This deficiency is not peculiar to this experiment, however, since virtually all studies of plant tolerance to soil salinity are similarly handicapped. Salt distribution in an irrigated saline soil is always exceedingly variable, since water cannot move into and through a soil without transporting the solutes. Consequent to this phenomenon, a sample taken in a saline soil might prove quite meaningless as to indicating the soil salinity in the absorbing zone of the roots. Even though the sample were taken in what is normally regarded as the absorbing zone of the roots, it is quite possible that a pocket of soil directly below the irrigation furrow would be much lower in salt and would therefore be the region of water absorption. Thus, the average stress upon the plant may not nearly approach what would be indicated by the average salt content of the soil in the absorbing root zone, because of the fact that water is primarily absorbed in regions of minimum salt content *(6, 13)*.

In order to evaluate the soil-moisture stress upon the plants grown under the various degrees of salinity in these experiments, an involved mathematical method was developed to arrive at the rate of change in soil-moisture stress over the absorbing zone of the roots during an irrigation interval *(26)*. The method permitted taking into account variations in salt content with depth in the container of soil. Integration of the relation between moisture stress and time permitted an evaluation of the average moisture stress upon the roots during an irrigation interval. The distribution of salt in a container was derived from the data in figure 5. These data, converted to osmotic-pressure values of the soil solution by means of the relationships in figure 7, are given in table 9. The average rates of change in moisture content per container of soil with time during an irrigation interval are shown in figures 9 to 12. The values for moisture content shown are those observed during the month of August. The corresponding rates of change in soil-moisture stress with time for the 14 experimental conditions also are shown in figures 9 to 12.

TABLE 9.—*Calculated osmotic pressure of the soil solution at 12 percent moisture*

Treatment	Horizon (in thirds)			Treatment	Horizon (in thirds)		
	Upper	Middle	Lower		Upper	Middle	Lower
	Atmospheres	*Atmospheres*	*Atmospheres*		*Atmospheres*	*Atmospheres*	*Atmospheres*
OL	0.91	1.31	3.26	S_2L	0.65	2.64	6.1
OH	.71	.93	2.32	S_2H	.55	2.23	5.3
C_1L	1.88	7.3	13.2	S_4L	1.04	5.1	8.6
C_1H	1.12	4.75	16.0	S_4H	.75	3.9	8.5
C_2L	5.02	13.4	18.6	S_8L	4.3	8.9	11.7
C_2H	6.8	13.1	18.9	S_8H	2.0	8.8	12.9
C_4L	10.8	22.4	31.0				
C_4H	24.0	18.6	21.8				

The typical ranges in moisture content and moisture stress observed in the high and the low moisture-tension regimes of the 0-salt treatments are shown in figure 9, *A*. It is possible that the relatively small stress developed even in the OL treatment was effective in inhibiting growth of guayule. From figure 1 it may be seen that depleting the soil moisture to 14 percent would not have brought about much more than half an atmosphere of tension. Table 9 shows that appreciable quantities of salines had accumulated in the 0-salt cultures from the irrigation water; that is, a major part of the moisture stress shown in figure 9, *A*, was due to osmotic pressure. On the basis of sand-culture studies *(28)* this osmotic pressure may have been sufficiently high to inhibit growth of guayule.

Plants grown under the OH treatment developed a high stress—20 atmospheres—before being irrigated. Yet these plants at no time showed evidence of wilting. The tension on the soil moisture at the permanent-wilting percentage as determined by sunflower plants has been found to vary from 10 to 25 atmospheres *(4, 25)*. A xeromorphic species like guayule may stand even higher tension values before showing evidence of wilting. The fact remains, however, that guayule made considerably poorer

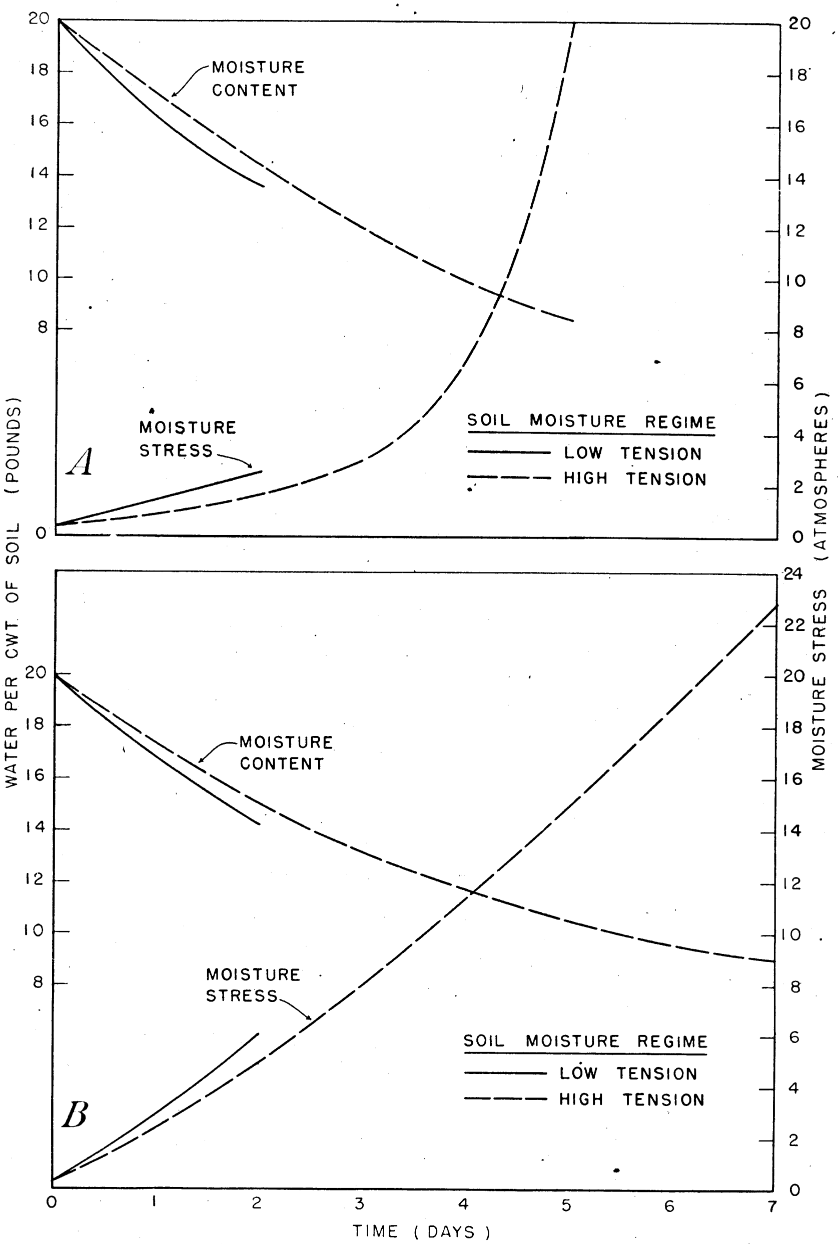

Figure 9.—Rate of change in moisture content and moisture stress during an irrigation interval within *(A)* the control (0-salt) cultures and *(B)* cultures containing 0.1 percent NaCl.

growth on the OH than on the OL treatment. It is evident that the high diffusion-pressure deficit developed in the soil moisture during the last day of the irrigation interval of the OH series would effect an increase in diffusion-pressure deficit within the tissue fluids of the plant. The development of such a stress would definitely inhibit growth processes *(27)*.

The average ranges in moisture content and moisture stress of the cultures containing 0.1 percent NaCl are shown in figure 9, *B*. The maximum stress developed in the C_1L cultures was more than double that shown for OL treatment, even though the difference in growth response of the respective plants was not large. The maximum stress developed in the C_1H cultures was only slightly greater than that shown for the OH treatment, yet the plants were only about half as large as those on soil to which no salt was added. A comparison of the stress-time curves for these two treatments shows that whereas this relationship is pronouncedly exponential in the OH cultures (fig. 9, *A*), it is nearly linear under the conditions of the C_1H treatment (fig. 9, ***B***). This means that over an irrigation interval the C_1H plants were subjected to a stress of more than 10 atmospheres during half the time in comparison to being subjected to such a stress for only a few hours, as found for the OH cultures.

The changes in moisture content and moisture stress in soil cultures containing 0.2 and 0.4 percent NaCl, respectively, are shown in figure 10. The curves for stress-time in the high moisture-tension regime are definitely convex upward, in marked contrast to the shape of the stress-time curve found for the OH treatment in figure 9, *A*.

This change in shape of the stress-time curves with increasing salt content of the substrate is considered to be of fundamental importance in the explanation of plant response to saline soils. Evidence indicates that a plant undergoes changes in its physiological status as the soil-moisture supply approaches the wilting percentage *(10, 11, 29)*. The rate at which internal changes may take place with respect to rate of change of external stress will condition the characteristics of the plant response. For example, owing to the hyperbolic nature of the moisture-sorption curve (fig. 1), the rate of change in external stress in a nonsaline soil may be so rapid just above the wilting percentage that physiological adjustments within the plant could hardly be expected to keep pace. Hence, the plant may develop the symptoms of wilting very suddenly. In a saline soil, it is evident from figure 10 that the rate of change in external stress may be low. Under such conditions the plant may be subject to a total soil-moisture stress that is equal to or in excess of the moisture tension at the wilting percentage for weeks at a time without the plant showing symptoms of wilting. Recent unpublished observations at this laboratory have confirmed this. Plants exposed to such conditions make practically no growth, the lower leaves abscise, but the conventional symptoms of wilting may not appear.

This interpretation of the importance of the rate of change in moisture stress just above the wilting percentage upon the

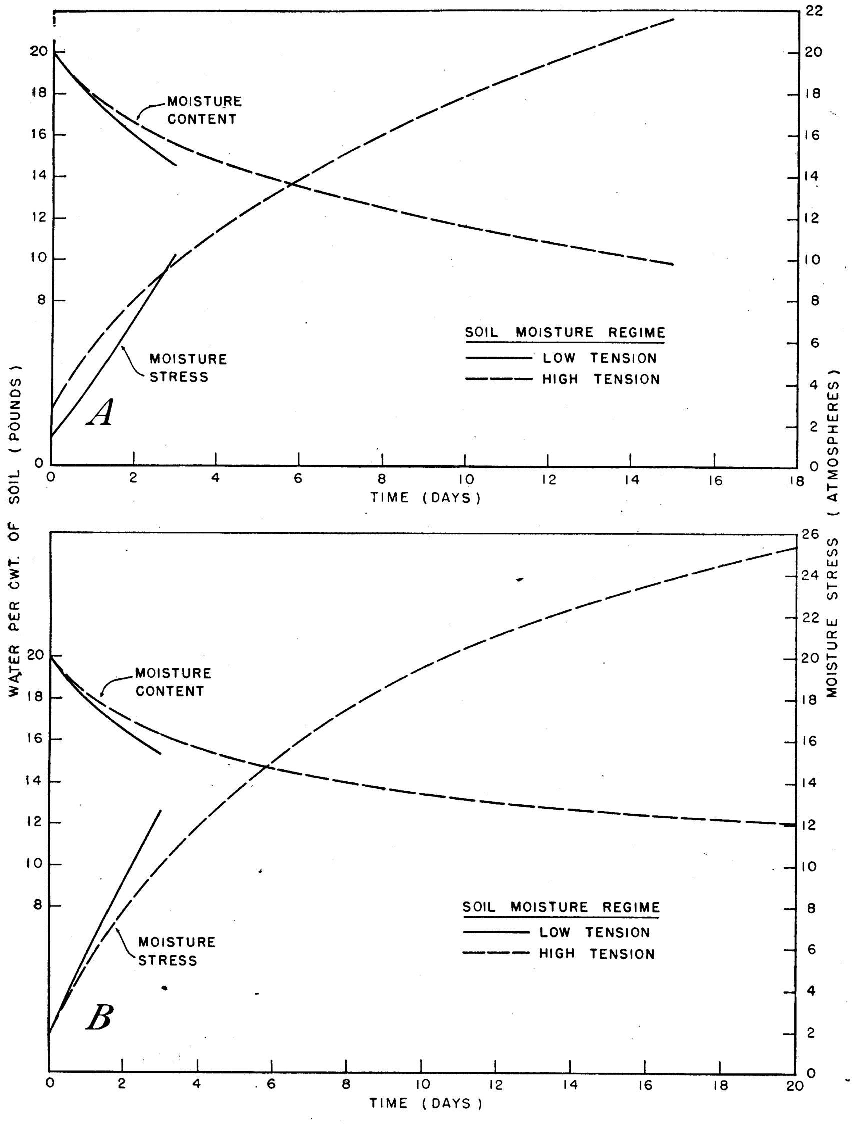

FIGURE 10.—Rate of change in moisture content and moisture stress during an irrigation interval within cultures containing (*A*) 0.2 percent NaCl and (*B*) 0.4 percent NaCl.

expression of symptoms of wilting by the plant is undoubtedly related to the very wide range in the energy values of the soil moisture at the wilting percentage found by Richards and Weaver *(19)* for soil samples on which wilting-range determinations have been made by Furr and Reeve *(8)*.

Figure 11 shows the rate of change in moisture content and moisture stress for the sulfate series of plants at both the low and

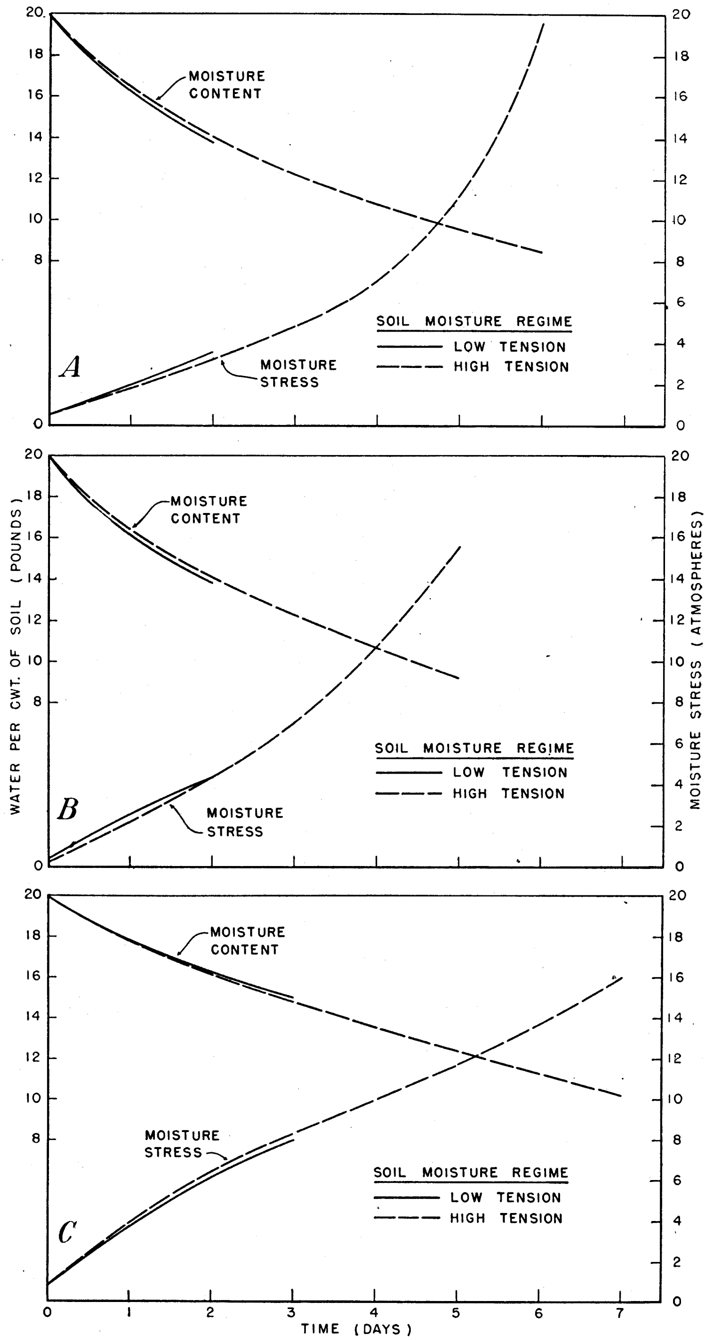

FIGURE 11.—Rate of change in moisture content and moisture stress during an irrigation interval within cultures containing (*A*) 0.2 percent Na_2SO_4, (*B*) 0.4 percent Na_2SO_4, and (*C*) 0.8 percent Na_2SO_4.

high moisture-tension regimes. Owing to the previously mentioned chemical changes that took place in the soil to which Na_2SO_4 was added, the shapes of the stress-time curves differ somewhat from those curves derived for treatments receiving comparable quantities of NaCl. Thus the time-stress curve for

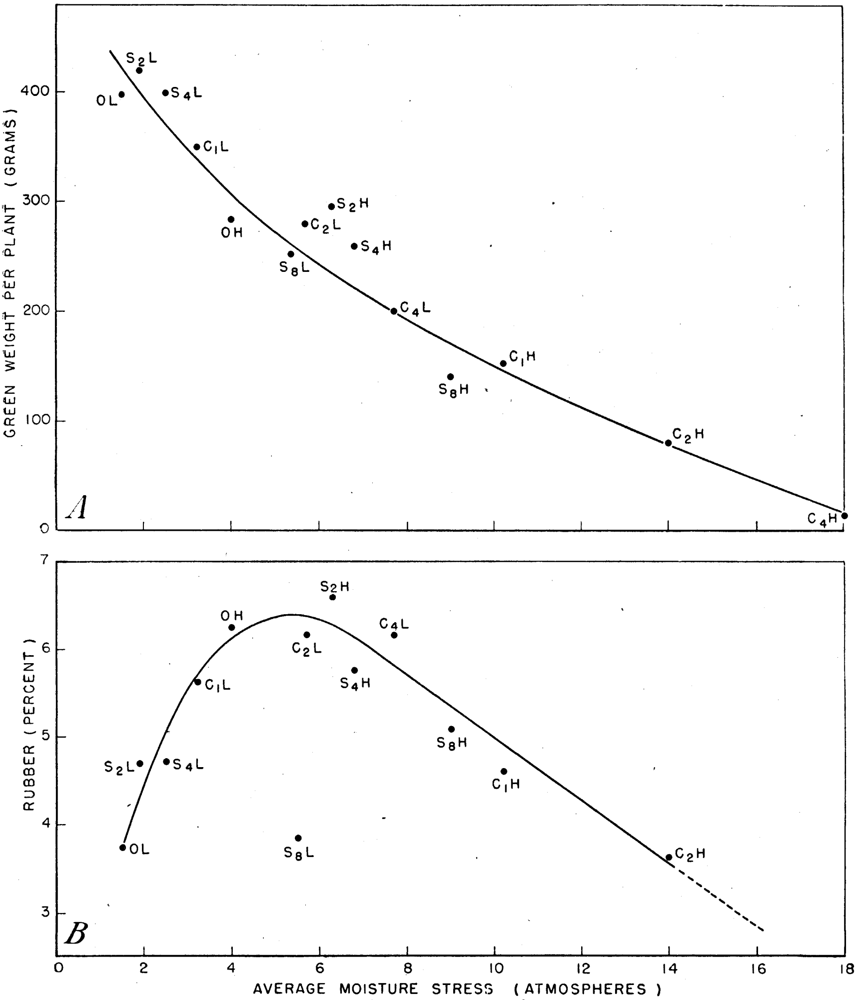

FIGURE 12.—Relation between the average moisture stress of the irrigation interval and (*A*) the growth of the plants and (*B*) the percentage of rubber in the millable bush.

the S_2H cultures (fig. 11, *A*) was more similar to the curve derived for the OH treatment (fig. 9, *A*) than for the C_1H cultures (fig. 9, *B*). This, of course, is consistent with the observation that growth response on the S_2H cultures was even slightly superior to that produced by the OH treatment and just about double the growth response observed under the C_1H conditions. On the other hand the trend of the stress-time curve for the S_8H cultures (fig. 11, *C*) is quite similar to that observed under the C_1H conditions, and the growth response of the guayule under these two conditions is almost identical (table 1).

It is possible to integrate the areas under the stress-time curves given in figures 9 to 11 and arrive at the average integrated moisture stress for an irrigation interval by dividing by the duration in days of the irrigation interval *(26)*. The average green weights of plants (tops) per treatment are plotted against the corresponding values for the average integrated moisture stress in figure 12, *A*. This relatively close relationship between average moisture stress and growth of guayule corroborates the findings of Wadleigh and Ayers *(27)* pertaining to a similar study in beans. It is further evidence that water availability to plants is conditioned largely by the total specific free energy of the soil moisture rather than by the status of one or more separate factors that affect the total free energy. The limitations of the method by which the average moisture stresses were calculated have been discussed by Wadleigh *(26)*. In view of these limitations, the closeness of the relationship observed in figure 12, *A*, is considered noteworthy as an endorsement of this method of approach to the water relations of plants growing in saline soils.

The observations on percentage of rubber in the millable bush are plotted against the respective observations for average soil-moisture stress in figure 12, *B*. That the observation for treatment S_8L is completely out of line with the others is obvious. It was mentioned with reference to figure 3, *A*, that the percentage of rubber in the millable bush of treatment S_8L was unexplainably anomalous and may represent an analytical error. The writers believe that the lack of coherence of this point with the others does not seriously detract from the validity of the general trend shown in figure 12, *B*.

It is evident that at the lower levels of moisture stress the percentage of rubber in the millable bush increased markedly with increase in stress. For example, the percentage of rubber in the OH plants was nearly double that of the OL plants. This is in line with the observations of Kelley and associates *(12)* that an increase in moisture stress increased the rubber content of guayule. In their work, however, increased moisture stress was induced largely by an increase in moisture tension, since they were working with a nonsaline soil. That is, treatments OL and OH of this report approximate the range of moisture stress covered in the studies of Kelley and others *(12)*.

It is evident from figure 12, *B*, that rubber percentage is increased at the lower ranges of moisture stress, whether the stress is induced by moisture tension or by osmotic forces in the soil solution. It is especially pertinent to emphasize that the results of this experiment, as presented in figure 12, *B*, show that if the moisture stress becomes really high, owing to a combination of both high soil-moisture tension and appreciable quantities of solutes in the soil solution, the trend of the relation between rubber percentage and moisture stress is reversed. These results suggest that the positive relationship between rubber percentage and moisture stress, as reported by Kelly and others *(12)*, is incomplete, inasmuch as it appears to hold for only the lower range of average moisture stresses.

The writers believe it is physiologically valid to expect a marked decrease in rubber percentage at really high levels of moisture stress. Obviously, rubber is a derivative of the primary photosynthate of the plant.

High moisture stresses have been found to influence the accumulation of photosynthate in other species *(20, 27)*. Furthermore, it was observed that when guayule plants were subjected to the higher levels of moisture stress studied, the lower leaves of the plants died at an abnormally higher rate. This condition cut down on the photosynthetic surface of the plants. It would logically follow that conditions inhibiting the accumulation of primary photosynthetic reserves would also inhibit the quantity of rubber synthesized.

SUMMARY

Guayule plants were grown in large containers holding 100 pounds of a Panoche loam in various cultures of which the salt content was established at 0, 0.1, 0.2, and 0.4 percent NaCl; and at 0.2, 0.4, and 0.8 percent Na_2SO_4.

Three different conditions of the soil-moisture regime were superimposed on each of the seven different salt levels:

1. Irrigated when only about 50 percent of the available water had been removed. (available water being taken as that present in the soil between the limits of the field capacity and the wilting percentage).
2. Irrigated when nearly all of the available water had been removed.
3. Irrigated according to schedule (1) during the first half of the experimental period and according to schedule (2) during the latter half.

Each salt-moisture level was thrice replicated.

Nursery-grown plants were transplanted to the soil containers on February 3 and harvested on December 1, 1943.

Growth of the plants was inhibited by increased degree of depletion of the available soil moisture prior to irrigation.

Increasingly larger quantities of NaCl in the soil were associated with a progressively greater decrease in plant growth within each soil-moisture regime. Additions of Na_2SO_4 were not associated with significant decreases in growth response unless in excess of 0.4 percent.

At low soil-moisture tension the presence of salt in the soil tended to be associated with an increase in percentage of rubber in the millable bush. With moisture regimes involving high tension, increasing soil salinity was associated with marked decreases in rubber percentage.

In general, there was a marked decrease in yield of rubber per plant with increasing salinity and increased moisture tension, the main exception being an increase in rubber with the presence of a small quantity of salt at low moisture tension.

Increasing soil salinity was associated with an increase in the quantity of irrigation water required to produce a given weight

of millable bush. Likewise, on an average, an increase in salinity necessitated a marked increase in the quantity of irrigation water per gram of rubber produced.

Surface irrigation of the soil containers caused a marked downward movement of the added salt.

Within a given irrigation regime, vegetative growth of the plants was closely associated with the specific conductance of the extract of the saturated soil from the surface horizon (upper 5 inches).

Analyses of the extracts of the saturated soils and of the displaced soil solutions showed that interactive effects had taken place between added solutes and the original soil components. Addition of NaC1 to this Panoche loam resulted in a displacement of some of the calcium from the exchange complex by sodium, with the result that calcium made up as much as 50 percent of the cations in the soil solution. Addition of Na_2SO_4 to this soil also resulted in the displacement of calcium by sodium in the exchange complex, and as a result solid phase $CaSO_4$ of low solubility was formed. This chemical reaction caused a lower concentration of the soil solution than would be expected on the basis of the quantity of salt added.

A close relation was noted between the specific conductance of the extract of the saturated soil (32 percent H_2O) and that of the displaced soil solution obtained at 12 percent moisture. Owing to the effect of additional solid phase $CaSO_4$ coming into solution with dilution, the above relationship for the Na_2SO_4-treated soil differed from that of the soil receiving NaCl. A close relation existed between the specific conductance of the displaced soil solution and the osmotic pressure of this solution.

The rate of change in the total soil-moisture stress (sum of moisture tension plus osmotic pressure of the soil solution) was determined for representative irrigation intervals for the various treatments. It was found that the shape of the derived stress-time curves differed markedly, depending on the degree of salinity of the soil; and the specific shapes of the different curves bore a definite relation to the nature of plant response in the nonsaline and saline soils.

The average moisture stress during an irrigation interval was determined. It was found that growth inhibition of guayule was closely related to the total moisture stress, regardless of whether this stress was due predominately to moisture tension or to osmotic pressure of the soil solution.

The percentage of rubber in the millable bush was found to be closely related to the average moisture stress over an irrigation interval. This relationship was found to be markedly positive over the lower ranges of moisture stress. It was immaterial to rubber accumulation whether this moisture stress was induced by tension or by osmotic pressure. The curve for this relation, however, showed a decided maximum. Average moisture stresses exceeding 6 atmospheres were progressively deleterious to rubber accumulation.

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